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The Impact of Nitrogen Eutrophication on Caribbean Coral Reefs: A Review

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Abstract

Coral reefs are declining in the Caribbean region due to a variety of reasons. Nitrogen from agriculture, sewage, and other anthropogenic sources is polluting coastal waterways and represents one major threat to reef health. The effects of nitrogen eutrophication on coral reefs was investigated in this review. Nitrogen pollution slows calcification, changes photopigment concentrations, accelerates coral disease rates, increases coral-algal competition, and reduces coral reproduction and recruitment. To conserve these important ecosystems and sustain the variety of services they provide, nitrogen loading to coral reef ecosystems must be reduced.

Introduction

Nutrient enrichment is causing coral reef degradation and mortality across the world. Coral reefs thrive in high quality coastal waters and are sensitive to changes in water quality, such as influxes of nitrogen (Baker et al. 2013). The magnitude of these influxes, which are also referred to as nitrogen eutrophication, is often anthropogenic. Nutrients can enter waterways from agriculture, sewage, and atmospheric deposition (Baker et al. 2013). Resulting reef degradation may occur through changes in coral calcification, light reduction, and competition due to macroalgal growth, decreased coral recruitment and reproduction, and changes in coral diversity (Fabricius 2005). Reefs at the highest risk of pollution-caused damage include those on deeper slopes, reefs in poorly flushed locations, commonly disturbed reefs, and those lacking herbivorous fishes (Fabricius 2011).

Effects on hard coral are of particular concern as these species are typically reef-builders due to the accumulation of their calcium carbonate skeletons over time. A meta-analysis of Caribbean coral decline using 65 studies and encompassing 263 sites in the Caribbean basin found that average hard coral cover

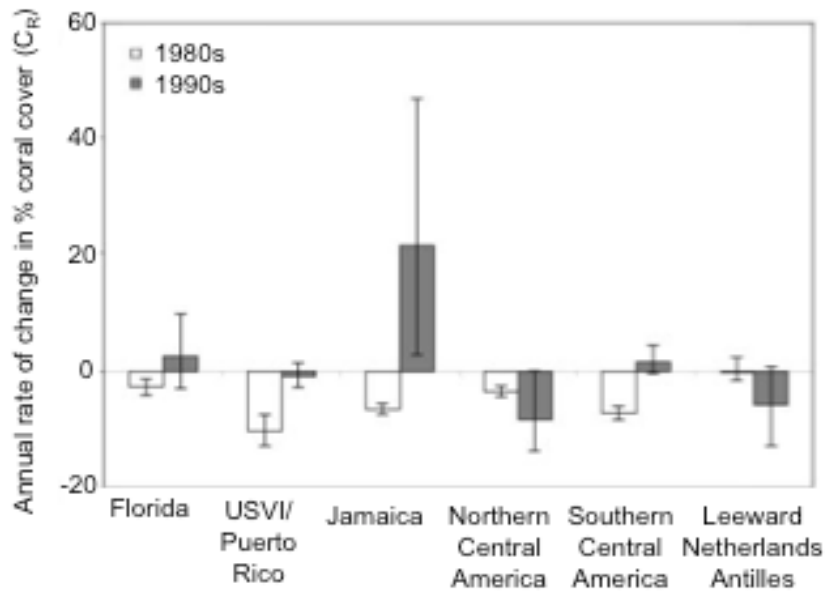


Figure 1. Variability in mean rate of coral cover change in 1980 (open bars) and 1990 (shaded bars). Bootstrap-generated 95% confidence intervals are shown. Sample sizes for the 1980s and 1990s, respectively, are: Florida: 4 and 64; U.S. Virgin Islands/Puerto Rico: 33 and 26; Jamaica: 29 and 7; northern Central America: 12 and 29; southern Central America: 8 and 3; and Leeward Netherlands Antilles: 4 and 12. (Figure source: Gardner et al., 2003)

was reduced by 80% in three decades (Gardner et al. 2003). Local factors, including eutrophication, were attributed as the predominant causes of this decline. Any slowed rates of declines or apparent recoveries, such as in Jamaica, portray a potentially overly optimistic trend as the results only reflect changes in total coral cover and not changes in community composition (Fig. 1). Other studies have revealed changes in reef communities, such as a shift in dominance by reef-builders like *Acropora* (ie. elkhorn and staghorn) and

Montastrea to non-reef builders (Gardner et al. 2003).

The protection of coral reefs is necessary if we are to ensure the preservation of the ecosystem services reefs provide. For example, about 9×10^6 tons of fishery biomass per year are extracted from coral reefs, amounting to approximately 12% of the amount obtained globally (Zarco-Perelló et al. 2013). Beyond supporting commercial fishing, coral reefs also protect our coasts, provide animal protein, promote tourism, and supply the ocean with abundant biodiversity (Kennedy et al. 2013). The calcium carbonate skeletons generated by coral create a habitat relied upon by diverse species, and the natural erosion of these structures generates the critical sand accumulation needed by many beach ecosystems (Kennedy et al. 2013). The continuation of these services is in jeopardy as 20% of the world's coral reefs have been lost already, making this an imminent problem (Zarco-Perelló et al. 2013). This review relates the broad problem of nitrogen eutrophication to the Yucatán Peninsula specifically and goes on to synthesize the information available on the effects of nitrogen pollution on coral communities throughout the Caribbean. Consequences discussed include physiological effects on calcification and photopigments, accelerated disease rates, increased coral-algal competition, and effects on reproduction and recruitment. I place particular

emphasis on hard coral; however, I also discuss soft coral species. Ultimately, this review seeks to determine whether nitrogen eutrophication is a significant factor contributing to observed coral declines, with particular focus on the Caribbean region.

Nitrogen Eutrophication

Nitrogen eutrophication causes negative consequences for marine foodwebs, coastal economies, and more broadly for many ecosystems, making nitrogen management a vital concern. Increased algal growth and the creation of anoxic dead zones in marine ecosystems are the most obvious negative effects of eutrophication (Bricker et al. 2008). A less obvious but equally important consequence occurs when nitrogen is denitrified by microbes, resulting in the emission of nitrogen in gaseous forms. Many of these gases have negative, far-reaching effects, such as NO_x and N₂O, which are notable greenhouse gases (Hirsch et al. 2006). Increased nitrogen loading into ecosystems stimulates the rate of denitrification and the production of these greenhouse gases (Kinney and Valiela 2013).

Humans are responsible for approximately doubling the amount of available nitrogen cycling in terrestrial ecosystems (Vitousek et al. 1997), and therefore nitrogen management is of concern to many fisheries and land managers. Conventional monitoring of water quality for total nitrogen concentration is a major weakness of nitrogen management solutions because it does not discriminate between natural and anthropogenic sources (Baker et al. 2013). In addition to the anthropogenic sources mentioned previously, nitrogen concentration can also fluctuate in aquatic ecosystems due to nitrogen fixation, upwelling, and rapid biological assimilation (Baker et al. 2013). One method of determining the source of nitrogen is to use stable isotope ratios in organisms. This method often indicates that anthropogenic sources are significant contributors to nitrogen levels in coastal waterways. Such is the case in the Yucatán, a peninsula in southeastern Mexico.

Land-based sources of nitrogen pollution in the Yucatán ultimately end up in the ocean. Seven years of data from Quintana Roo, Mexico, revealed that sewage alone accounted for 42% of nitrogen values in the biomass of the common sea fan, *Gorgonia ventalina* (Baker et al. 2013). The rapid growth and construction occurring in this area is built upon a karst aquifer, which discharges into *cenotes* and surface fractures, ultimately eroding into lagoons (Baker et al. 2013). In these lagoons, seawater mixes with groundwater, resulting in a transfer of any pollutants into coral reef habitats. As many residential areas do not have wastewater treatment, nitrogen can dissipate into groundwater when it rains and end up in the ocean at levels detectable over 1 km from shore (Baker et al. 2013). Additionally,

local tourism accounts for a large proportion of nitrogen loading into the ocean (Herrera-Silveira et al. 2004, Baker et al. 2013). For example, some large resorts in the Yucatán pump sewage directly into the aquifer (Baker et al. 2013). In the northern Yucatán, shrimp farm effluent at four sites was also a contributing factor as people fertilize shrimp ponds with nitrates (Herrera-Silveira et al. 2004). It is therefore unsurprising that nitrogen is polluting coral reef ecosystems. However, it is less obvious whether this pollution is directly responsible for the decline of Caribbean coral reefs. For example, the small hard coral and octocoral colonies found in the Sisal Reefs off the northern Yucatán coast display densities from 0.35 colonies/25 cm² to 0.96 colonies/25 cm², signaling that these communities are under stress (Zarco-Perelló et al. 2013). Based on the large amount of nitrogen pollution in the area, it is likely that nitrogen is causing this stress. The direct effects of nitrogen on coral must be investigated to determine if they are severe enough to account for coral degradation and extinction events.

Calcification

The effect of nitrogen on calcification leads to coral reef degradation. Calcification is the process by which hard corals build up calcium in the form of calcium carbonate (CaCO₃) and increase skeletal mass. Nitrate level was found to be the most important factor for degraded Caribbean reef carbonate budgets, with a 10% increase in nitrate leading to a 33% decline in net carbonate production (Kennedy et al. 2013). Similarly, the rate of coral growth off the coast of Barbados in nitrogen-polluted waters was lower than rates from nearby reefs in more pristine waters (Szmant 2002). Likewise, a study using the hard coral species *Montastraea annularis* and *Porites porites* found that skeletogenesis decreased by 50% in both species when exposed to nitrate enrichment at levels of 5 and 20 μM, as seen in Figure 2 (Marubini and Davies 1996). Reduction in skeletal formation is logical as nitrate addition also causes zooxanthellae density to increase (Marubini and Davies 1996). Higher numbers of these algae lead to a reduction in available carbon for calcification as the algae utilize carbon in the water for photosynthesis. When carbonate levels in the water are high, nitrogen does not cause growth reduction, providing evidence for this competition-based explanation (Marubini and Thake 1999). The competition over inorganic carbon for algal photosynthesis and host skeletogenesis when nitrate levels are high may be intensified in areas lacking water movement, where the recharge of CO₂ is restricted.

The evidence for nitrogen-based effects on calcification is convincing, but is not yet complete. Some studies report no change in growth with ammonium or nitrate enrichment (Szmant 2002), and therefore a consensus on whether nitrogen always affects calcification has not been reached. It is possible that studies finding

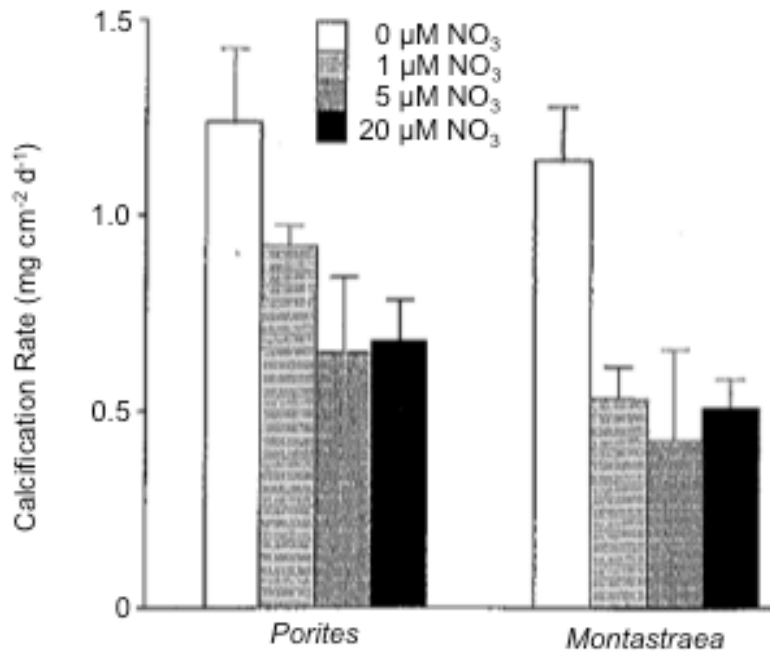


Figure 2. Daily calcification rate (mean \pm 1 SD) of *Porites porites* (n = 32) and *Montastrea annularis* (n = 18) at four different nitrate concentrations. Incubation in photostat chambers occurred for 40 and 30 days, respectively. (Figure source: Marubini and Davies, 1996)

no effect were confounded by the presence of high carbonate levels in the water. Additionally, one commonly cited shortcoming of laboratory studies is that the nutrient concentrations used are much higher than those actually found at polluted reefs. However, even the exceedingly low nitrate concentration of 1 μM led to significant effects in some cases, as seen in Figure 2 (Marubini and Davies 1996). Further studies should address whether elevated CO_2 associated with climate change will reduce competition for inorganic carbon within

coral reefs, as an availability of carbon for both host and algae may lead to an increase in growth when excess nitrate is present. If this is true, the combination of eutrophication and elevated CO_2 may actually increase reef growth, particularly if the coral species are able to utilize bicarbonate (HCO_3^-) in addition to carbonate (CO_3^{2-}), which is typically used by coral. It is possible that the decrease in carbonate and increase in bicarbonate that occurs when CO_2 dissociates into water will negatively affect coral (Marubini and Thake 1999). However, bicarbonate has recently been shown to be utilized by coral for calcification and possibly photosynthesis (Comeau et al. 2013). Therefore, the elevated dissociation of CO_2 into the ocean may not be as harmful to reefs as previously believed.

Photopigments

Studies regarding the effect of nitrogen pollution on photosynthesis are severely lacking. Many studies have found that increased dissolved inorganic nitrogen (DIN) increases the concentration of chlorophyll *a* per zooxanthellae and the rate of photosynthesis (Fabricius 2005). Likewise, chlorophyll *a* and *c*₂ concentration increased in each zooxanthellae cell of one hard coral species, causing the coral to

appear darker (Marubini and Davies 1996). Although several studies report increased photosynthetic rates, none address the implications of these changes or whether there is a quantifiable limit to the photosynthetic rate achieved. At high photosynthetic rates, it seems likely that high levels of oxygen could be produced in the coral's tissue. Studies addressing this possibility should determine whether oxygen could reach dangerous levels and whether these levels are affecting coral. If high photosynthetic rates are not affecting coral, how are coral counteracting these nitrogen-caused changes? Coral can decrease photosynthetic rate under high light intensity (Hoegh-Guldberg and Jones 1999), but it is not yet evident whether these inhibitory mechanisms are also used to decrease the elevated photosynthetic rates associated with nitrogen pollution.

Because nitrogen directly increases pigments in zooxanthellae, the concentration of photosynthetic pigments can act as an early-warning indicator for nitrogen pollution (Fabricius 2005). While abundant macroalgae can also hint at high nitrogen levels, the presence of macroalgae itself does not necessarily mean nitrogen levels are high. However, the presence of macroalgae can also cause an increase in coral pigment concentrations even when nitrogen levels are not high, making these levels a somewhat unreliable indicator of nitrogen pollution. Low light levels caused by shading from macroalgae can lead to increased pigment density in coral as the coral attempt to sustain photosynthetic rates (Fabricius 2011). If macroalgae are not substantial enough in the environment to cause significant shading and subsequent low-light acclimatization by coral, an increase in zooxanthellae pigments could signify nitrogen-polluted waters. This represents another area requiring future research that will reveal more about the interplay between nitrogen and photosynthesis in coral reef ecosystems.

Rates of Coral Disease

Nitrogen pollution affects rates of coral diseases, which have increased over the past two decades (Bruno et al. 2003). Infection rate and disease transfer are accelerated by increased nutrient concentrations in experimentally and naturally infected coral colonies, possibly because marine fungi and bacteria are nitrogen limited (Bruno et al. 2003). Two widespread Caribbean coral epizootic diseases were tested, including aspergillosis, which affects *Gorgonia ventalina*, and yellow band disease, which affects the important reef-builders *Montastraea annularis* and *Montastraea franksii* (Bruno et al. 2003). The field experiments occurred on a fore-reef at Akumal on the Yucatán Peninsula, where yellow band disease occurs in 4 to 17% of *Montastraea* species. Higher prevalence, up to 91%, can be found in other Caribbean reefs (Bruno et al. 2003).

Similarly, experiments focusing on a major reef-building coral in the Caribbean, *Siderastrea siderea*, also provide evidence that nitrogen eutrophication accelerates coral disease rates (Voss and Richardson 2006). *S. siderea* was artificially infected in the laboratory and exposed to nitrate concentrations up to 3 μM , resulting in a doubling of black band disease progression (Voss and Richardson 2006). Increased nutrient concentrations *in situ* also doubled the rate of black band disease progression and coral tissue loss (Voss and Richardson 2006). This disease occurs worldwide and infects 64 scleractinian species, causing tissue losses that expose the coral skeleton, which often becomes colonized by macroalgae (Voss and Richardson 2006). Further experimental studies could be used to supplement these findings and more *in situ* observations should investigate possible correlations between nitrogen-polluted sites and disease rates, especially since both have likely increased in coastal waters since these studies were conducted.

Coral-Algal Competition

Algal blooms are increasing across the world due to coastal eutrophication and have major impacts on coral reefs (Lapointe et al. 2005). When these macroalgae are not controlled by grazers, even tiny increases in dissolved inorganic nutrients lead to increased algal productivity (Fabricius 2011). These blooms deplete oxygen in the water column when they decay and can proliferate so much that they create enormous algal masses. These masses block sunlight, which is essential for coral reef survival as coral needs sunlight to perform photosynthesis and keep up with the energy demands of calcification (Fabricius 2011).

Like many locations in the Caribbean, coral reefs off the coast of Florida have experienced several macroalgal blooms recently due to nitrogen eutrophication (Lapointe et al. 2005). High nitrogen conditions are more favorable for macroalgae, which have rapid growth rates, than for coral (Fabricius 2011). These blooms compete with coral for space, restrict gas exchange (Fabricius 2011), and lead to anoxic/hypoxic conditions, which result in the death of hard and soft corals (Lapointe et al. 2005). The primary source of the nitrogen causing Florida's harmful algal blooms is land-based sewage rather than natural upwelling (Lapointe et al. 2005). This has been attributed to the fact that the highest $\delta^{15}\text{N}$ values occurred on shallow reefs, which would be expected if the source was land-based. Further support involves the finding that NH_4^+ concentrations are elevated during non-upwelling periods and are the preferred source of nitrogen for macroalgae, as opposed to upwelled NO_3^- . Regardless of the source, it is clear that nitrogen eutrophication is a major cause of algal blooms, which result in degraded coral reefs.

Because macroalgae proliferate in high nitrogen conditions, coral recovery following disturbances may be low. Coral cover off of Yawzi Point at St. John in the U.S. Virgin Islands showed that disturbance events can lead to a transition from coral to macroalgal cover (Edmunds 2002). In a ten-year period, coral cover declined by more than 50% at Yawzi Point, during which time two hurricanes affected the reef (Edmunds 2002). *Montastraea annularis* in particular was damaged by the storms, which led to reduced reef structure and complexity (Edmunds 2002). Meanwhile, macroalgal growth increased 12-fold (Edmunds 2002). Replacements such as the one seen at St. John are occurring across the Caribbean and will likely be exacerbated as nitrogen pollution increases. While Yawzi is not subject to many local anthropogenic effects relative to other reefs, reefs that are disturbed by humans have been more strongly affected by the replacement of coral with macroalgae (Edmunds 2002). As discussed previously, high light and/or nitrogen conditions allow macroalgae to proliferate much more rapidly than coral and subsequently block sunlight. Light is essential for the recruitment of new coral larvae. Light intensity and spectral composition control the settlement of these larvae, and the reduction in light caused by macroalgae reduces the depth at which larvae can settle (Fabricius 2011). Low recruitment rates hinder recovery following disturbance events (Fabricius 2011). Therefore, algal blooms are detrimental to coral reefs following hurricanes. Further studies should investigate the role of nitrogen specifically in coral-algal competition following disturbance events.

Reproduction and Recruitment

Successful reproduction of scleractinian corals, reef builders that generate a hard skeleton, is critical if reefs are to be maintained throughout time, especially in frequently disturbed ecosystems. When corals are stressed, they redirect their energy and resources from reproduction to repair mechanisms or other functions (Harrison and Ward 2001). Because coral reproduction has a low stress tolerance, poor water quality impacts the fitness of corals. Gametes of scleractinian corals are exposed in the water and are therefore vulnerable to pollutants. For example, *Porites porites* produced fewer larvae in polluted reefs and had a skewed male to female sex ratio (2:1) compared to reefs in higher quality water (Harrison and Ward 2001).

Specifically, terrestrial nitrogen runoff makes it difficult for reefs to recover from disturbances due to effects on coral reproduction and recruitment. Coral recruiting species and the number of young recruits decreased with increasing eutrophication in Barbados reefs (Harrison and Ward 2001). Acroporid corals (notable framework builders in reefs) have lower fecundity, egg size, fertilization

rates, and embryo development at even very low levels of nitrogen concentration ($1 \mu\text{M NH}_4$) (Fabricius 2005). Gametes from the brain coral, *Goniastrea aspera*, have a significantly lower chance of developing into regular embryos and a higher chance of being deformed from ammonium concentrations as low as $0.5 \mu\text{M}$ (Harrison and Ward 2001). These effects become stronger as concentration increases. Therefore, reef degradation demonstrated at these slightly increased nitrogen levels will likely be intensified in reefs exposed to higher levels of land-based nitrogen pollution.

Conclusions

In this review, the potential contribution of nitrogen eutrophication to observed coral declines was investigated with particular emphasis on the Caribbean region. Based on the effects of nitrogen pollution on coral calcification, disease rates, coral-algal competition, reproduction, and recruitment, eutrophication is a significant contributor to current declines. Even relatively low nitrogen levels considerably reduce calcification rates and slow reef growth. More studies regarding calcification should be conducted with the aim of avoiding confounded results from the presence of high carbonate levels in water. Calcification research should also address whether elevated atmospheric CO_2 will reduce competition for inorganic carbon within coral reefs or only harm the reefs through ocean acidification. Low levels of nitrogen pollution also increase the growth of macroalgae, which compete with coral for light and space, creating anoxic dead zones and intensifying reef degradation. The role of nitrogen in coral-algal competition following disturbance events should be investigated experimentally and *in situ*. Excess nitrogen also increases coral epizootic disease rates, leads to abnormal development, and decreases coral fecundity, egg size, and fertilization rates. The mechanism underlying nitrogen-driven increases in coral disease rates should be investigated, and an evaluation of nitrogen-polluted sites should compare nitrogen levels to disease rates. Consequences due to nitrogen-based changes in photopigment concentration remain unknown and represent a large knowledge gap requiring further research.

While several aspects of nitrogen's effects on coral must still be investigated, it is clear that nitrogen eutrophication causes detrimental effects that substantially contribute to coral degradation and extinction events. Current knowledge of these effects combined with results of the many studies yet to be performed will provide an abundance of useful information for conservationists and ecosystem managers in the Caribbean and elsewhere. Immediate action should be taken to reduce nitrogen loading in coral reef ecosystems in order to sustain their many services, such as supporting commercial fishing, protecting our coasts,

providing animal protein, promoting tourism, and supplying the ocean with abundant biodiversity and critical habitat.

References

- Baker, D. M., R. E. Rodriguez-Martinez, and M. L. Fogel. 2013. Tourism's nitrogen footprint on a Mesoamerican coral reef. *Coral Reefs* **32**:691-699.
- Bricker, S. B., B. Longstaff, W. Dennison, A. Jones, K. Boicourt, C. Wicks, and J. Woerner. 2008. Effects of nutrient enrichment in the nation's estuaries: a decade of change. *Harmful Algae* **8**:21-32.
- Bruno, J. F., L. E. Petes, C. Drew Harvell, and A. Hettinger. 2003. Nutrient enrichment can increase the severity of coral diseases. *Ecology Letters* **6**:1056-1061.
- Comeau, S., R. C. Carpenter, and P. J. Edmunds. 2013. Coral reef calcifiers buffer their response to ocean acidification using both bicarbonate and carbonate. *Proceedings of the Royal Society B: Biological Sciences* **280**.
- Edmunds, P. J. 2002. Long-term dynamics of coral reefs in St. John, US Virgin Islands. *Coral Reefs* **21**:357-367.
- Fabrizius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* **50**:125-146.
- Fabrizius, K. E. 2011. Factors determining the resilience of coral reefs to eutrophication: a review and conceptual model. Pages 493-505 *Coral reefs: An ecosystem in transition*. Springer.
- Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* **301**:958-960.
- Harrison, P., and S. Ward. 2001. Elevated levels of nitrogen and phosphorus reduce fertilisation success of gametes from scleractinian reef corals. *Marine Biology* **139**:1057-1068.
- Herrera-Silveira, J. A., F. A. Comin, N. Aranda-Cirerol, L. Troccoli, and L. Capurro. 2004. Coastal water quality assessment in the Yucatan Peninsula: management implications. *Ocean & coastal management* **47**:625-639.

- Hirsch, A. I., A. M. Michalak, L. M. Bruhwiler, W. Peters, E. J. Dlugokencky, and P. P. Tans. 2006. Inverse modeling estimates of the global nitrous oxide surface flux from 1998–2001. *Global Biogeochemical Cycles* **20**.
- Hoegh-Guldberg, O., and R. J. Jones. 1999. Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. *Marine Ecology Progress Series* **183**:73-86.
- Kennedy, E. V., C. T. Perry, P. R. Halloran, R. Iglesias-Prieto, C. H. L. Schönberg, M. Wisshak, A. U. Form, J. P. Carricart-Ganivet, M. Fine, and C. M. Eakin. 2013. Avoiding Coral Reef Functional Collapse Requires Local and Global Action. *Current Biology*.
- Kinney, E. L., and I. Valiela. 2013. Changes in delta N-15 in salt marsh sediments in a long-term fertilization study. *Marine Ecology Progress Series* **477**:41-52.
- Lapointe, B. E., P. J. Barile, M. M. Littler, and D. S. Littler. 2005. Macroalgal blooms on southeast Florida coral reefs: II. Cross-shelf discrimination of nitrogen sources indicates widespread assimilation of sewage nitrogen. *Harmful Algae* **4**:1106-1122.
- Marubini, F., and P. S. Davies. 1996. Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. *Marine Biology* **127**:319-328.
- Marubini, F., and B. Thake. 1999. Bicarbonate addition promotes coral growth. *Limnology and Oceanography* **44**:716-720.
- Szmant, A. M. 2002. Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? *Estuaries* **25**:743-766.
- Vitousek, P. M., J. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: causes and consequences. Ecological Society of America Washington, DC, US.
- Voss, J. D., and L. L. Richardson. 2006. Nutrient enrichment enhances black band disease progression in corals. *Coral Reefs* **25**:569-576.

Zarco-Perelló, S., M. Mascaro, R. Garza-Perez, and N. Simoes. 2013. Topography and coral community of the Sisal Reefs, Campeche Bank, Yucatan, Mexico. *Hidrobiologica* **23**:28-41.